STUDIES ON FRESHWATER BRYOZOA. III.

The Development of *Lophopodella carteri* var. *typica*

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INTRODUCTORY

As previously stated in Study I, *Lophopodella carteri* var. *typica* occurs in pond habitats on the under side of *Nymphaea* leaves and on *Vallisneria*, *Elodea*, *Potamogeton* and other pondweeds. It produces reproductive bodies known as statoblasts. These are of one type—free, annulated. They germinate and give rise to new colonies. Colonies of this form were collected at Squaw Harbor (Put-in-Bay) and East Harbor in the southwestern part of Lake Erie and taken into the laboratory. Their behavior under laboratory conditions was noted. Their released statoblasts were collected and in time germinated. The growth and development of the resultant colonies and their production of another crop of statoblasts was carefully noted and recorded. Since the observations were made on living material, no attempt will be made in the present study to discuss the histology of the various processes.

METHODS

In collecting, the colonies were either gently taken off the lily pads or lily stems with a scalpel blade or else the whole lily pad was brought into the laboratory and the colonies left undisturbed on it. They were kept in fresh lake water in fingerbowls. The water was changed daily to insure sufficient food supply and proper conditions for the polypides. As statoblasts were released by the colony they were put into a Syracuse watch glass (with water) until the time of germination. After germination, the watch glasses with the germinating statoblast or polypide were immersed in a finger bowl. This made possible microscopic study of the zooecia with the least disturbance.

Colonies which were collected during the summers of 1932 and 1933 were kept in the Stone Biological Laboratory—not

far from the collecting site—and later (in September) transferred to the laboratory at Ohio State University (Columbus, Ohio). Their behavior and development under laboratory conditions was studied until the succeeding summers. The animals were kept alive with at first daily, then twice weekly, changes of medium. The medium in which these animals were kept was simply greenhouse tank water and some organic debris from around the bases of aquatic plants which were grown in the greenhouse tanks. Some of the organisms which occurred in the water were Planaria, Ostracoda, Copepoda, Oligochaeta, Rotifera, Gastropoda and Protozoa, in addition to plant material.

OBSERVATIONS

Colonies of *L. carteri* were collected during the entire summer season. The earliest date for the finding of mature statoblasts was July 20 (1933). After that time they were found in almost every collection. However, in the 1932 collections (from Squaw Harbor) no mature statoblasts were recovered from the colonies until September 24 although developing statoblasts were found as early as August 19. The latest day for release of statoblasts in the laboratory from the comparatively small number of colonies of the 1932 collections was November 22. Statoblast germinations occurred from November 19, 1932, until the supply of statoblasts was exhausted (February 9, 1933). The succeeding year, germinations were continuous until the end of March, when observations were discontinued.

THE DEVELOPMENT OF A COLONY FROM A STATOBLAST

The dormant period of statoblasts has been given attention by relatively few workers—Braem, Brooks, Brown, Graupner, Kraepelin, Marcus, Oka and Wesenberg-Lund. These workers have given some very interesting observations on germination and dormancy of statoblasts of some of the following species: *Plumatella repens*, *P. coralloides*, *Cristatella*, *Fredericella*, *Pectinatella magnifica* and *Pectinatella gelatinosa*. Some workers insisted that freezing was necessary before the germination of statoblasts. Others believed that that was not necessary. The length of the rest period is also variously given. Brown (1933) has given a very good account of germinations under various conditions. Brooks (1929) concluded that *Pectinatella*

"statoblasts develop steadily from the time they are formed until the polypides are fully formed, just as buds do." This conclusion came as a result of observations upon the germination of statoblasts under different temperature and environmental conditions. A similar condition exists in *Lophopodella*, at least as concerns those statoblasts which developed in the laboratory. Statoblasts of *L. carteri* var. *typica* which were collected or which developed from the August 25, 1933, collection have hatched continually until the termination of observations—March 22, 1934, and there still remained a large number which might have hatched had they been permitted to develop to the proper stage.

The rest or dormant period of a statoblast is interpreted as the period between its release and its germination. Brown (1933) defined germination as the separation of the two valves and the protrusion of the polypide. Rest periods of *L. carteri* statoblasts varied from 34 to 137 days. The germination of these reproductive bodies was undoubtedly hastened by the subjection to laboratory temperature conditions. Figures for statoblasts under natural conditions of extremes of temperature would probably be considerably different.

GERMINATION

The first visible indication that a statoblast is ready to germinate is the splitting of the chitinous processes at the extremities of the valves and the appearance of crooked dark ridges on the capsule surface. The splitting is first noted at the tips of the processes. This continues to the base of the spines, then the valves also begin to split. The peculiar nature of the spined processes is clearly shown when they have split, for it is then that one notices that the barbs of the processes of one valve do not correspond to or coincide with the barbs of the corresponding processes on the other valve. This splitting process may take considerable time, more than a week, but just how much longer has not been determined.

After the valves have split to a slight degree, the embryo may be seen as a rounded ball or mass of tissues, grayish-white in color. The length of time which is required before this mass of tissues becomes a full-fledged polypide depends upon a great many factors such as the potentialities inherent within the statoblast, the nature of the medium in which the statoblast germinates, the temperature and other physical and biological

factors. Under unfavorable conditions, this mass of tissue never reaches the polypide stage but simply degenerates. For the past two years I have been unable to rear colonies from statoblasts which have hatched late in the year (November and December). However, those which germinated in January, February and March produced colonies. The failure in the first instance may have been due to improper care or to the fact that some of the statoblasts germinated prematurely and the polypides lacked sufficient vitality to carry them through the budding stages. However, this is merely supposition.

The time required before this ball of germinating tissue protrudes as a contractile and motile structure from between the valves is very short. It may be only a day or two, depending upon the factors previously mentioned. For want of a more descriptive term I shall use the term employed by Brooks—("mucous pad")—for this protruding structure. (Brooks used the term in connection with *Pectinatella*.) When this first appears, it can be divided into two distinct areas—an outer, clear whitish cellular rim and the remaining denser, grayish, more granular, inner portion. The distinction between these two areas is more marked in the early stages of the polypide than in the more advanced stages. This basal portion is very contractile and adhesive. If it is watched for a period of time, undulations, contractions or occasional movements may be observed. By this structure the polypide and the valves of the statoblast are attached more firmly to the substratum. This portion of the body wall may change its shape from an indefinite rounded mass to a finger-like projection or to a bi- or tri-lobate protrusion. It is very turgid, resembling a collodion sac filled with liquid.

As yet, the valves of the statoblast are quite close together. In the meantime the polypide is developing between the valves, hidden from view.

The polypide protrudes its tentacles beyond the edge of the valves in about two or sometimes three days after the "base" has appeared. The polypide is apparently well developed but still not fully grown. Its tentacles are much shorter than those of an adult. The same fact holds for the digestive tract. The distance from the lophophore to the invaginated fold is much smaller than in the adult. Even the number of tentacles may be fewer in the young than in the mature polypide.

If one observed the individual very closely and under proper illumination one can see the very delicate transparent ectocyst. It terminates at the invaginated fold. When the individual moves or contracts, the ectocyst is thrown up in a number of wrinkles or folds.

As the polypide continues to develop and enlarge, the valves of the statoblast are pushed farther and farther apart. The base begins to lose its distinctive appearance and gradually becomes more and more like the remainder of the polypide.

BUDDING

Brooks (1929) attempted to rear *Pectinatella* polypides, noting that they lived for two weeks upon yolk material and that they could be kept alive for six weeks but that they remained as single polypides instead of forming colonies. The trouble may have been with the food supply, because in the case of *Lophopodella*, as soon as the food supply was increased and the right kind of food used, the polypides began to multiply in number.

In the case of *Lophopodella* very complete records were kept of two colonies in particular, although a number of others were watched less closely. For convenience, we shall call these two colonies *A* and *B*. These colonies were all of the second generation, that is, were hatched from statoblasts which came from the colonies collected in Squaw Harbor.

Table I gives the number of individuals which were present in each colony at any particular time.

The interval between germination of a statoblast and the evagination of the second polypide is relatively long—19, 21, 38, and 43 days (figures for four colonies). The interval between the evagination of the second and third polypides was 8 days for Colony *A* and 3 days for Colony *B*. The intervals between the third and fourth polypides was 2 days for *A* and 3 days for *B;* between the fourth and fifth polypides, 4 days each for *A* and *B;* between the fifth and seventh polypides, 3 days for *A* and 1 day for *B;* between the seventh and eighth polypides, 1 day each for *A* and *B;* between the eighth and twenty-seventh polypides, 7 days for *A* and 8 for *B;* between germination and the thirty-seventh polypide of Colony *B* and between germination and the forty-fifth polypide of Colony *A* was 68 days and 70 days respectively.

TABLE I

Date	Rate of Budding		Statoblasts Released	
	Colony *A*	Colony *B*	Colony *A*	Colony *B*
	Number of individuals	Number of individuals		
I- 7-1933	Just hatched			
I- 9	1	Just hatched		
II-14	2	1		
II-21	2	2		
II-22	3	2		
II-24	4	3		
II-27	4 plus 3 buds	4		
II-28	5	4		
III- 1	5	4		
III- 3	7	5		
III- 4	8	7		
III- 5	12	8		
III- 6	13	9		
III- 7	15; statoblasts developing	10		
III- 8	20	14; statoblasts developing		
III- 9	24; about 9 statoblasts developing	16		
III-10	25	18		
III-11	27	22		
III-13	32; numerous statoblasts in colony; some with a dark brown central capsule	27		
III-14	40; colony distinctly tri-lobate	32; colony tri-lobate, one lobe showing signs of subdivision		
III-15	42; three main lobes in colony, each subdivided into two; about 24 developing statoblasts	33		
III-16	43; four main lobes	34		
III-17	44	34		
III-18	45; many statoblasts present in colony	37		
III-19	44; colony divides into two colonies; one polypide degenerated after the division	37; colony in five lobes, ready to divide	2	2
III-20		Colony divided in two		
III-21	One colony divided		1	1
III-22			1	
III-23		Another division		
III-24			3	
III-27			8	3
IV- 3			16	8
IV- 4			3	
IV- 6				1
IV-6 to V-25			6	1
V-31				1
VI-19	The *A* and *B* colonies, some of their statoblasts and some young colonies which had hatched between April 8 and June 18, 1933, from some of the statoblasts produced by Colonies *A* and *B* were transferred from the Zoology laboratory in Columbus, Ohio, to the Stone Biological Laboratory on Lake Erie.			
VI-20	The colonies did not survive the rough handling en route.			

Approximately 58 and 59 days elapsed between the germination of the statoblasts which produced Colonies *A* and *B* and the appearance of young, developing statoblasts in the two colonies. Exactly 40 days later (on the 89th day of the existence of Colony *B*) three statoblasts of Colony *B* germinated in the laboratory. The first statoblasts of Colony *A* to germinate did so when the colony was 110 days old. Of the 40 statoblasts produced by Colony *A*, 15 germinated between April 27 and June 18, 1933. Of the 17 produced by Colony *B*, 9 germinated between April 8 and May 15.

Although Colony *A* hatched two days before *B* and showed developing statoblasts earlier, these statoblasts did not begin to germinate until over three weeks after the first ones of Colony *B* had germinated. This is most likely a matter of individual variation.

The foregoing account has dealt principally with the asexual form of reproduction in this variety. Sexual reproduction needs careful study in order to make the life cycle story complete.

CONCLUSIONS

1. *Lophopodella carteri* var. *typica* was observed through two generations and to the beginning of the third, in the laboratory.

2. Careful accounts were kept of the development of two colonies in particular—the date of their germination, the time intervals between evagination of succeeding polypides and the rate of development, release and germination of statoblasts from these colonies.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. Two developing statoblasts in a colony of the August 29, 1932, collection.

Fig. 2. Side view of the statoblasts pictured in Fig. 1.

Fig. 3. The statoblasts in a slightly more advanced stage.

Fig. 4. A later stage in the development of a statoblast. The statoblast was drawn on October 17, 1932, and shows the lobate edges of the float. The edges had not as yet sufficiently differentiated to show the characteristic barbed processes. There were eight lobes on one side and nine on the other in this particular specimen.

Fig. 5. A still later stage in the development of a statoblast. This diagram shows a thin gelatinous covering or sac investing the statoblasts. Several statoblasts with such an investment were observed in late October in colonies of the September 25, 1932, collection. The processes at the ends are well differentiated.

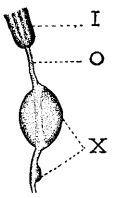
Fig. 6. A statoblast end bearing the barbed processes. The air cells of the float are also shown.

Fig. 7. A sketch of Colony *B* just preceding division. The statoblasts are shown as being somewhat concentrated in two lobes. To simplify the drawing, the polypides are roughly figured in the retracted state. The strip of coenoecial tissue connecting the three lobes becomes narrower and longer, due to the muscular activity of the polypide, particularly of the muscles of the body wall, until eventually, the connection breaks and the colony has divided into two parts.

Fig. 8. An enlarged view of the splitting of a barbed process at the extremity of the statoblast. The barbed process when superficially observed appears single but closer inspection shows that it is composed of two similar halves, one-half from each valve, and that the barbs of the halves do not necessarily coincide, but that there may be some overlapping.

ABBREVIATIONS

A—Ciliated tentacles.
B—Lophophore.
C—Tentacular crown.
D—Region of anal opening.
E—Rectum.
F—Esophagus.
G—Tentacular sheath.
H—Invaginated fold region. Musculature omitted.
I—Stomach.
J—Bud.
K—Retractor muscles.
L—Ectocyst.
M—Endocyst.
N—Body wall.
O—Funiculus.
P—Float.
Q—Capsule.
R—Barbed processes.
S—Statoblast valve.
T—Coenoecium.
U—Lobe.
V—Zooecium.
W—Epistome.
X—Statoblast.
Y—Temporary base or "mucous pad" (Brooks).
Z—Gelatinous covering.



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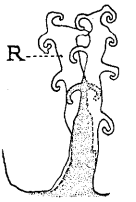

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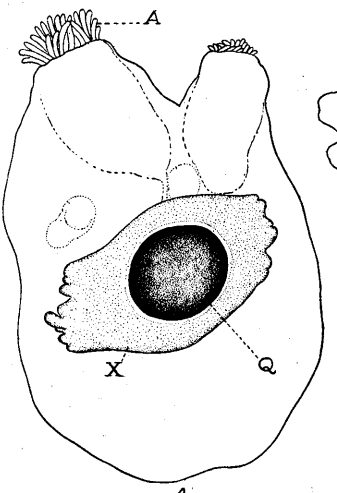

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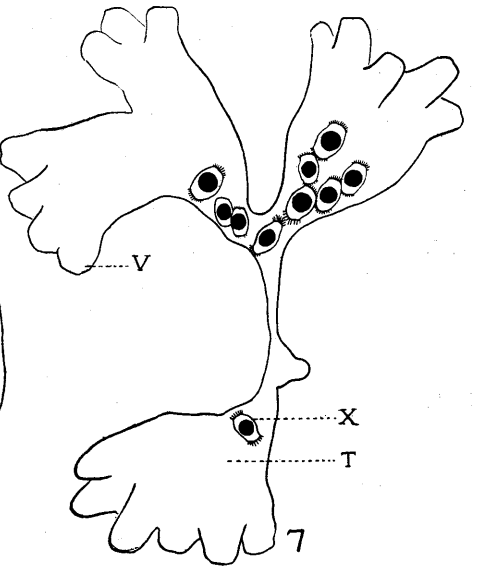

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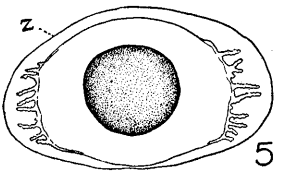

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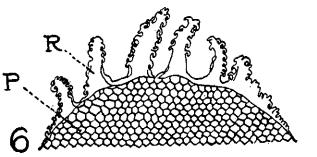

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EXPLANATION OF PLATES

PLATE II

Fig. 1. Colony *B* three days after hatching (hatched on February 9, 1933). The basal part is contractile and motile; yolk granules present.

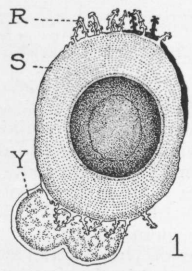
Fig. 2. Colony *B* as it appeared on February 13, showing the protruding tentacular crown of the first individual. When the surroundings were disturbed, the polypide quickly withdrew from sight between the two statoblast valves.

Fig. 3. Colony *B* on February 14. The tentacles numbered 52 in *B* and 56 in *A* at this time. This view of the tentacular crown shows the relative lengths of the tentacles on the arms of the lophophore and about the oral region at this particular stage. The epistome is evident although the mouth is not shown clearly. A number of features of the polypide are omitted in the figure, the purpose of the sketch being merely to show the growth of the colony.

Fig. 4. Colony *A* as it appeared on February 1, 1933. It was hatched on January 7. A developing bud is shown in the body wall. The statoblast valves remained attached to the polypide until February 18. Older zooecia differ from the young in having longer tentacles, a larger lophophore, a longer digestive tract and a greater length of polypide between the lophophore and the invaginated fold. The ectocyst is shown as the outer extremely delicate and transparent membrane.

Fig. 5. A small colony, showing the general arrangement of the zooechia. Not all polypides can be shown from any one angle of observation, hence, there are more polypides present in the colony than pictured. In this figure, the tentacular crowns have been cut away and the internal organs of the polypides have been omitted for the sake of clarity.

(See page 464 for Explanation of Abbreviations)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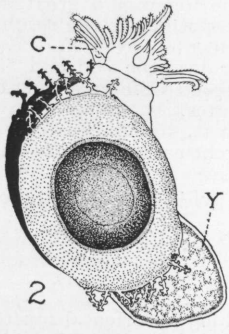
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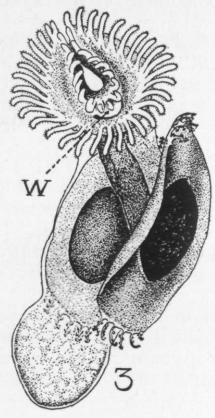
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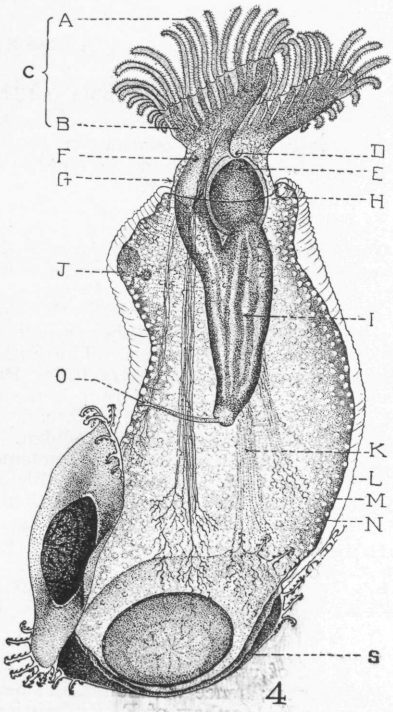
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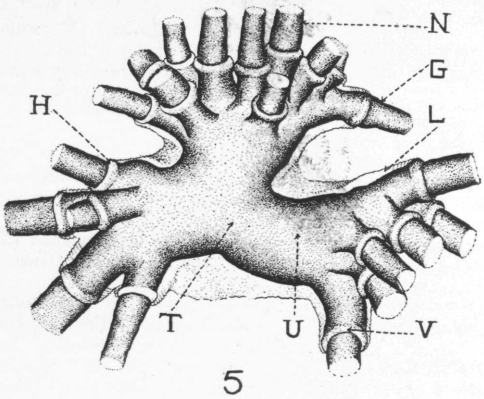
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